

Wolverines and their prey in southern Norway¹

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Abstract: Wolverines (*Gulo gulo*) recolonized the Snøhetta plateau in southern Norway in 1976–1979 after an absence of over 50 years. This is presently the southernmost part of the wolverine's distribution and the only area where it coexists with wild reindeer (*Rangifer tarandus*) in western Europe. Other, larger predators in the Scandinavian ecosystem, the wolf (*Canis lupus*), lynx (*Lynx lynx*), and brown bear (*Ursus arctos*), have been absent from the area since the beginning of this century. We monitored wolverine numbers, reproduction, and diet during the denning period and studied the effects of abundance of different prey species on wolverine reproduction. Although there were differences in productivity among maternity dens, the main factor influencing the number of wolverine cubs surviving was the abundance of small rodents ($p = 0.0002$). Although small rodents constituted the main factor explaining variation in cub numbers, the basic prey during the denning period was reindeer. Hares (*Lepus timidus*) accounted for a significant but stable part of the diet during the denning period. The wolverine was an important predator on sheep (*Ovis aries*), but we found no evidence that sheep are an essential part of its diet.

Résumé : Au cours de la période 1976–1979, le Carcajou (*Gulo gulo*) est réapparu sur le plateau de Snøhetta, dans le sud de la Norvège, après plus de 50 ans d'absence. C'est là la partie la plus australe de la répartition des carcajous et la seule région où ces animaux cohabitent avec des Rennes (*Rangifer tarandus*) sauvages en Europe de l'ouest. Les autres prédateurs de l'écosystème scandinave, certains plus gros, le Loup gris (*Canis lupus*), le Lynx roux (*Lynx lynx*) et l'Ours brun (*Ursus arctos*), sont absents de la région depuis le début du siècle. Nous avons étudié l'abondance des carcajous, leur reproduction et leur régime alimentaire au cours de la saison passée au terrier, et tenté de déterminer les effets de l'abondance des différentes espèces de proies sur la reproduction du Carcajou. Bien que la productivité enregistrée dans les différents terriers « pouponnières » se soit avérée variable, le principal facteur déterminant du nombre de jeunes survivants était l'abondance des petits rongeurs ($p = 0,0002$), mais la principale proie au cours de la période de mise-bas n'en restait pas moins le Renne. Le Lièvre variable (*Lepus timidus*) constituait une portion importante et stable du régime alimentaire au cours de la période de mise-bas. Le Carcajou s'est avéré un important prédateur du mouton *Ovis aries*, mais rien ne nous permet de croire que le mouton soit un élément essentiel du régime alimentaire du Carcajou.

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Introduction

The wolverine (*Gulo gulo*) is the largest terrestrial mustelid and is one of four large carnivores found in Scandinavia, along with the brown bear (*Ursus arctos*), wolf (*Canis lupus*), and lynx (*Lynx lynx*). These large carnivores have traditionally been regarded as pests because of their predation on domestic animals and other desirable herbivores. The number of bounties paid by the state decreased dramatically for all carnivores from 1870 until the enactment of protective legislation in 1973 for southern Norway and in 1982 for northern Norway. The larger predators (wolf, lynx, and brown bear) were hunted nearly to extinction (Sørensen et al. 1986; Landa 1986; Swenson et al. 1995). The brown bear and wolf have not yet been allowed to recover.

Until the beginning of this century, the wolverine was distributed throughout most forest and mountain areas as far

south as the southernmost counties of Norway (Johnsen 1928) and south-central Sweden (Lönnberg 1936). The species became totally protected in Sweden in 1968 and in southern Norway in 1973. Protection during the breeding period was introduced in northern Norway in 1975, and the species became totally protected throughout Norway in 1982. Protection was granted because, by this time, wolverines were scarce and threatened with extinction (Myrberget and Sørungård 1975; Ahlén 1977). There is good evidence that the population has increased since protection was introduced (Heggberget and Myrberget 1980; Ahlén 1981; Landa and Skogland 1995). Today wolverines are found mainly in mountainous areas in the northern parts of Norway and Sweden.

Wolverines are polyphagous, which enables them to switch between different food sources when one prey becomes scarce. In Scandinavia, the wolverine is primarily a scavenger on large ungulates (Haglund 1966). Wolverine distribution is sympatric with that of reindeer (*Rangifer tarandus*, both wild and domestic), which constitutes its most important winter food source (Pulliainen 1968, 1988; Myhre and Myrberget 1975; Semenov-Tyan-Shanskii 1982). Hares (*Lepus timidus*), ptarmigan (*Lagopus* spp.), and small rodents are also significant foods in winter (e.g., Pulliainen 1968; Myhre and Myrberget 1975), and may be the most important foods during summer (Myrberget and Sørungård

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1979; Magoun 1987). Larger animals in the wolverine's diet are probably obtained mainly as carrion (Magoun 1987; Banci 1987, 1994), but the wolverine can prey heavily on domestic sheep (*Ovis aries*) (Olstad 1945; Myrberget and Grotnes 1969; Kvam et al. 1988; Mortensen 1995; Børset 1995) and domestic reindeer (Björvall et al. 1990). Wolverine predation on wild reindeer has been documented only as isolated cases from the Snøhetta plateau. Preliminary evidence suggests that wolverines mainly kill old female reindeer in poor condition (Skogland 1989; Skogland et al. 1991; Skogland 1994).

We investigated the importance of small mammals and large herbivores as prey species to determine the main driving forces in the population dynamics of wolverines.

Study area and methods

The Snøhetta wild reindeer region in central southern Norway was recolonized by wolverines in 1976–1979 (Landa and Skogland 1995). The wolverine is the largest predator remaining in this area, which is the only remaining area where wolverines interact with wild mountain reindeer in Scandinavia. The wolverine population in Snøhetta has been assessed nine times since 1979, based on snow tracking (Kvam 1979, 1980; Kvam and Sørensen 1981, 1983; Overskaug et al. 1986; Sørensen and Kvam 1986; Kvam et al. 1987; Røskoft 1988; Landa and Skogland 1989; Loen 1991). After 1990, monitoring has been supplemented by radio tracking of wolverines in the area. All sightings or observed indications of wolverine hunts or scavenging activity were recorded, and when reindeer were preyed upon, mandibles were collected and age was estimated from tooth cementum (Grue and Jensen 1979). Numbers of wolverine maternity dens and observations of females with cubs, or of cubs alone, have been recorded annually since 1979, when the first denning activity was recorded. Dens were distinguished by area; that is, they had to be at least 10 km from other known locations to be defined as a new den. Dens were considered to be active when a female was observed using the location (February–April) or a female was seen at the locality together with cubs during May–September. All observations from the public (not scientific personnel) were evaluated by interviewing the observer.

An index of average small-rodent abundance, ranging from 1 (lowest) to 3 (highest), was obtained through an evaluation of field observations made by wardens and scientific personnel, who reported a subjective estimate of abundance of microtines (*Microtus* spp., *Lemmus lemmus*, *Clethrionomys* spp.) and birds preying upon small rodents, i.e., the rough-legged buzzard (*Buteo lagopus*), short-eared owl (*Asio flammeus*), hen harrier (*Circus cyneus*), and kestrel (*Falco tinnunculus*). Beginning in 1991, this index was supplemented by data from the terrestrial monitoring areas (TOV) project, which has one study site in the central part of the Snøhetta plateau (Kålås et al. 1995).

To estimate the effect of variation in the abundance of small rodents on wolverine reproduction, while controlling for potential effects of previous reproduction on the number of cubs produced in a particular year, we used the following autoregression model (Box et al. 1994):

$$[1] \quad X_i = aX_{i-1} + by_i + c_i + \varepsilon$$

where X_i is the number of cubs from a particular maternity den/year, y_i is the small-rodent index, $i = A, B, \dots, I$ is the den, and a , b , and c_i are parameters. This removes possible dependency between successive years in X_i . The long-term average cub number is represented by c_i in den i . We also tested for the effects of previous reproduction, X_{i-1} , and the effects of other variables (large

herbivores). Variables were removed from the model when $p > 0.10$. Note that this model also assumes that the random change in cub number between successive years, ε , is normally distributed, which could be questionable for discrete count data like these. When data from a previous year were missing, we assumed that no reproduction had taken place. Some maternity dens were active without producing any cubs. An autoregression model similar to [1] was used to test for possible effects of reindeer on the number of active maternity dens and also wolverines. We used the same approach as above with numbers of wolverines and active dens, respectively, as X_i on the small rodent index, reindeer winter population, and reindeer harvest. Because reindeer are harvested during autumn and are therefore probably most important to wolverines as stored resources (reindeer remains from human hunting), we used the reindeer harvest by human hunters in the autumn, prior to the wolverine denning, and the estimated numbers of wolverines as the variable in [1].

In June, after dens were vacated by female wolverines and their surviving cubs, we collected scats from all den sites located throughout the area. The scats were analysed by the frequency of occurrence method (Myhre and Myrberget 1975), and identifiable items of bones, hair, or feathers were classified as either reindeer, small rodent, bird, sheep, or mountain hare. The median percent occurrence of small rodents within scats and prey remains from sampled dens was compared with the small-rodent index.

The size of the reindeer population has been estimated several times since World War II, mainly from total counts of large herds photographed from small airplanes (Skogland 1985). When total counts were not available, numbers were estimated on the basis of calf recruitment and age-structure data. Calf production, determined from annual aerial counts, was defined as the ratio of live calves to live does ≥ 1 year of age. The counts were made 1 month after calving (20 June – 20 July) in 1979–1995 (Skogland 1985). Age structure was estimated from analysis of tooth cementum layers (Grue and Jensen 1979) from hunter-killed reindeer in 1982, 1983, 1984, 1986, and 1991.

Results

Small-rodent abundance in the wolverine diet

During the study we recorded 48 active maternity dens that were located at 9 distinctive and evenly distributed sites throughout the area. The most used den site produced an annual average of 1.35 cubs during the 17-year study period, whereas the least productive den was only used once and produced no cubs. A maximum of 4 active maternity dens were observed during a given year. Successful wolverine reproduction in a given year was influenced by den site but not by the number of cubs raised successfully in previous years, which has therefore removed from the model. However, the small-rodent index was positively related to the number of surviving cubs ($p = 0.0002$; Table 1, Fig. 1). The small-rodent index was not positively correlated with the number of wolverines ($F_{[1,5]} = 1.31$, $p = 0.31$) or active maternity dens ($F_{[1,14]} = 0.07$, $p = 0.80$). The frequency of small rodents, weighted by number of scats in each den, averaged 34%, but was greater at maternity dens with surviving cubs (51%) than at those that did not produce cubs (15%; Mann–Whitney U test, $df = 1$, $U = 5.0$, $p = 0.04$). Also, the frequency of small rodents in scats at dens was positively correlated with the small-rodent index ($r_s = 0.93$, $n = 7$ years, $p = 0.003$; Fig. 2).

Hares composed a substantial part of the wolverine diet during the denning period and occurred in 24% of sampled

Fig. 1. Recorded active wolverine maternity dens (A–I), number of surviving cubs, and small-rodent abundance in summer in Snøhetta, February–September in 1979–1995.

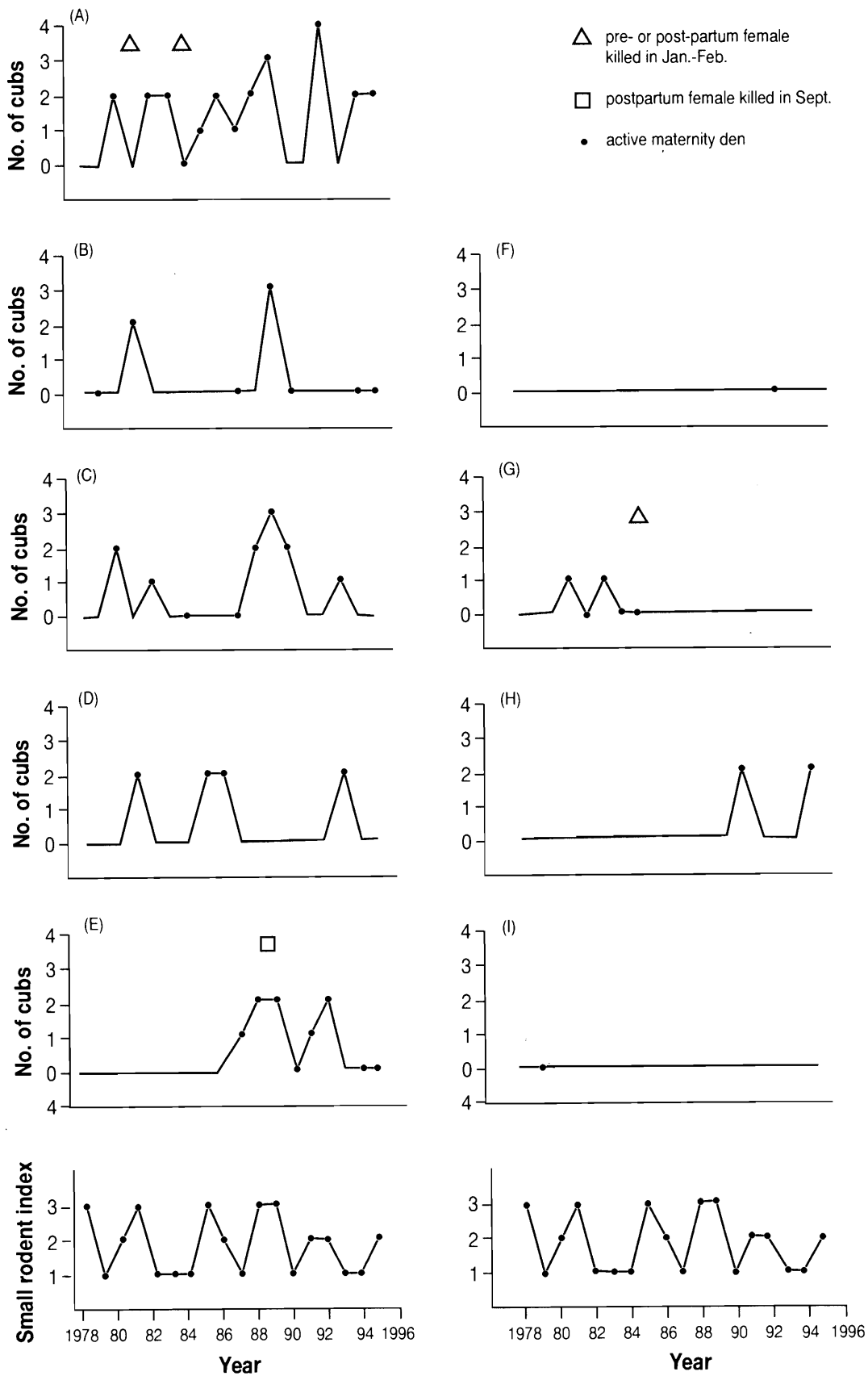


Fig. 2. Relationship between small-rodent abundance in summer and median frequency of occurrence of small rodents in scats collected at maternity dens.

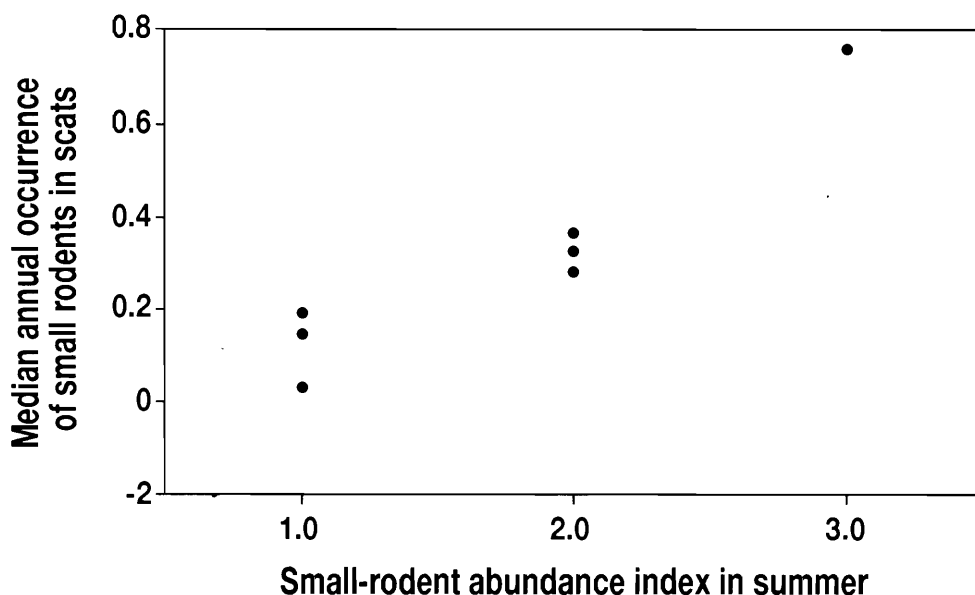


Table 1. Results of the autoregression model, controlling for effects of previous reproduction on the number of cubs produced in a particular year and the average difference in cub numbers between dens A–I.

Parameter	df	Estimate	SE	F	P > F
Intercept	1	-1.6019	1.1046		
b (rodent index)	(1,37)	0.5904	0.1411	17.51	0.0002
c _A (avg. in den A)	(8,37)	1.6645	0.8512	3.00	0.0106
c _B	1	0.5085	0.8668		
c _C	1	1.2509	0.8634		
c _D	1	1.4652	0.9149		
c _E	1	0.8033	0.8822		
c _F	1	0.2919	1.1387		
c _G	1	0.0420	0.8774		
c _H	1	1.7076	1.0047		
c _I	0	0	0		
Reindeer winter population	(1,37)	0.0004	0.0003	1.75	0.19

scats. The occurrence of hares in scats was fairly stable among dens (Table 2), and we found no correlation with annual number of active dens ($r_s = -0.19$, $n = 7$ years, $p = 0.68$) or number of surviving cubs ($r_s = 0.04$, $n = 7$ years, $p = 0.94$).

Large herbivores in the wolverine diet

The reindeer winter population in Snøhetta was reduced by human hunting from 3200 animals in 1981 to about 2100 animals in 1984 and has been kept at around 2000 since then. The wolverine population increased from about 7 individuals in 1979 to 14 in 1984, but declined the year after, and has varied between 11 and 17 since 1987 (Table 3). The mean ratio in winter was one wolverine to 170 reindeer. No positive relationship was found between the reindeer winter population and the number of wolverines ($F_{[1,2]} = 0.24$, $p = 0.67$) or between the reindeer winter population and the

recorded number of active wolverine maternity dens ($F_{[1,14]} = 2.17$, $p = 0.16$).

The number of reindeer killed during the autumn was not positively correlated with the number of wolverines ($F_{[1,2]} = 3.51$, $p = 0.20$), the number of surviving wolverine cubs ($F_{[1,33]} = 1.17$, $p = 0.28$) or the number of active wolverine maternity dens ($F_{[1,14]} = 0.11$, $p = 0.68$). The 5 wolverine-killed reindeer that we found were females between 11 and 14 years old and their teeth were severely worn (Skogland 1988).

Prey remains in collected scats were dominated by reindeer. Mean reindeer occurrence, weighted by number of scats at each den, was 84% (Table 2). Other ungulate foods identified were moose (*Alces alces*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*). A few domestic cattle remains were also identified.

Between 10 and 20% of the total number of sheep that die

Table 2. Percent occurrence of prey species in scats collected at wolverines maternity dens in Snøhetta, Norway, 1989–1995.

Den	Year	<i>n</i>	Reindeer	Rodents	Hare	Sheep	Birds	Remarks
A	1989	22	100	86	14	0	10	Raised 3 cubs
B	1989	21	100	60	23	14	0	Raised 3 cubs
C	1989	30	100	78	30	7	0	Raised 2 cubs
B	1990	33	91	15	32	12	0	Raised 2 cubs
C	1990	33	100	21	18	0	3	Not seen with cubs ^a
D	1990	12	85	0	15	0	0	Not seen with cubs ^a
C	1991	33	36	33	33	18	15	Raised 2 cubs
C	1992	36	100	38	46	0	0	Raised 2 cubs
E	1993	33	83	0	0	36	0	Not seen with cubs ^a
C	1994	33	63	18	48	33	0	Not seen with cubs ^{a,b}
C	1995	31	68	45	29	13	0	Not seen with cubs ^a
D	1995	30	83	10	0	17	0	One cub that died in June

^aDuring May–September.^bMinimum of one cub, partly eaten.**Table 3.** Recorded numbers of wolverines, active maternity dens, and cubs and data on legally and illegally killed wolverines, including sex and age where available, and natural mortality of wolverines on the Snøhetta plateau.

Year	No. of wolverines*	No. of active maternity dens*	No. of cubs in May–Sept.*	Legally and illegally killed wolverines	Natural mortality
1979	7	2	0	0	0
1980	—	2	4	1, age/sex unknown (illegal) M, 10 months	0
1981	12	3	5	F, 34 months, prepartum M, 10 months	0
1982	—	3	3	0	0
1983	—	2	3	F, 35 months	0
1984	14	3	0	F, 46 months, postpartum F, 35 months	M, 36 months
1985	9	3	3	F, 23 months, postpartum F, adult (illegal)	0
1986	—	2	4	F, 11 months F, 66 months, postpartum	0
1987	11	4	2	M, 6 months	0
1988	—	3	6	0	M, 28 months
1989	12	4	11	0	0
1990	—	3	2	M, age unknown, 1, age/sex unknown (both illegal)	0
1991	16	2	3	0	0
1992	12	2	6	1, age/sex unknown (illegal)	0
1993	—	3	3	0	0
1994	—	3	2	0	Cub, 2 months
1995	17	4	4	0	2 cubs, <3 months

*From Landa and Tømmerås (1996).

on open range in Snøhetta are found. Wolverine predation accounts for 50–85% of the mortality of these sheep (Børset 1995; Mortensen 1995). As the total annual loss during recent years has varied between 1600 and 2400, this suggests that between 800 and 1600 lambs are killed each summer by wolverines. Sheep occurrence, weighted by the number of scats in each den, was 13% (Landa and Tømmerås 1996). There were no negative correlations between the small-rodent index and the number of sheep lost ($r_s = -0.18$,

$n = 16$ years, $p = 0.52$), the occurrence of sheep in scats ($r_s = -0.37$, $n = 7$ years, $p = 0.42$), or the occurrence of sheep and reindeer in scats ($r_s = -0.66$, $n = 7$ years, $p = 0.10$).

Discussion

Because the litter size of wolverines increases with age, while the interval between litters decreases with age (Banci

and Harestad 1988), the variability among den sites in number of cubs produced, and also the number of active dens, could be affected by the age distribution of females in the population. However, such differences would be expected to change throughout the population over time and thus could not explain the long-term variation among den sites in our study. The most likely explanation for the observed variation therefore seems to be differences in habitat quality among den sites, which has also been observed in radio-tracked populations (Magoun 1985).

The importance of small-rodent abundance for medium-sized to large carnivores is rarely reported in the literature, but Banci (1994) considered wolverines to be too large to survive on small prey only. However, Myrberget and Sørungård (1979) found a strong correlation between an index of voles and wolverine litter size in northern Norway during 1960–1972, and Magoun (1987) reported that small rodents were the most significant part of the wolverine diet except during midwinter. We found that although wolverines at some dens reproduced better than others, the abundance of small rodents was a determining factor in reproductive success of wolverines on the Snøhetta plateau. The lack of other large predators in a system like Snøhetta could make wolverine reproduction more dependent on peaks in rodent cycles than would be expected in a more intact system. Wolverines have been observed scavenging remains of wolf kills (Björvall and Isakson 1982) and lynx kills (Haglund 1966). Björvall and Lindström (1991) speculated that the removal of more efficient predators like the wolf from the Scandinavian boreal ecosystem has had a negative effect on wolverine density because fewer secondary prey are now available for scavenging wolverines. This was supported by Landa and Skogland (1995), who found evidence for the food-limitation hypothesis in former and present Scandinavian wolverine populations, although present densities are lower and distribution is much more limited than before the turn of this century. It is therefore likely that the huge amount of food available during peaks in rodent cycles in general promotes wolverine reproductive success during peak years.

The predominance of reindeer remains in wolverine scats in Snøhetta is consistent with results of other studies in Fennoscandia (Haglund 1966; Myrberget 1968; Pulliainen 1968; Myrberget et al. 1969; Myhre and Myrberget 1975), based on wolverine tracking and stomach and scat analyses, all of which showed a high proportion of reindeer remains. The frequency of occurrence of prey remains, as revealed by scat or stomach analyses, hardly reflects the relative amounts of meat from different species. Most prey species found by scat and stomach analyses are detected from the occurrence of hairs. Wolverines explore all kinds of remains of dead animals and often forage on skin only, e.g., from reindeer (A. Landa, unpublished data). It is therefore likely that the frequency of occurrence of large prey detected in scats from scavenging wolverines would tend to overestimate the relative amount of reindeer in the diet.

Because wolverines became reestablished in our study area during a period when the reindeer population was reduced by human hunting, it would be surprising to find strong correlations between reindeer population parameters and wolverine parameters. Each autumn, people have witnessed wolverines scavenging reindeer killed by hunters, and

hiding the reindeer heads and skin that are usually left behind by the hunters. This, and remains of other large herbivores found at den sites, also indicate that denning females hoard to a large extent before breeding. The female's capacity to hoard or kill reindeer before and during cub rearing is therefore likely to influence cub survival.

Landa and Tømmerås (1996) found that even though the wolverine was a important predator on sheep, sheep numbers seemed to have little effect on wolverine numbers or reproduction. Sheep are released on mountain pasture in June and graze unattended until the beginning of September, when they are collected. Børset (1995) and Mortensen (1995) found that most documented wolverine predation occurred during the last few weeks of the grazing period. The onset of sheep predation occurs at a time when wolverine hoarding behaviour (Haglund 1966) is expected to increase before winter. Results from our study and that of Landa and Tømmerås (1996) indicate that sheep are not an essential part of the wolverine diet during the winter–spring denning period. It could be argued that because the wool is likely to fall off after sheep carcasses decompose, the relative amount of sheep meat/remains used by denning female wolverines could be underestimated in studies like this. However, wolverines kill mostly lambs (Landa et al. 1996). In the Snøhetta area it appears that about 70–100 lambs are killed by each wolverine during a season (Landa and Tømmerås 1996). The fact that wolverines did not kill more sheep during summer, when small rodents were less abundant and wolverine reproductive success declined, indicates that sheep are not an alternative to small rodents as prey. We therefore suggest that at least part of the wolverine predation on sheep might be “surplus killing,” that is, no part of the prey is utilized by the predator or by members of the same social unit (Kruuk 1972; Oksanen et al. 1985).

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References

- Ahlén, I. 1977. Om bevarande av hotade djurarter i Sverige. Skogshögskolan—Faunavård, Naturvårdsverket, Stockholm, Sweden.
- Ahlén, I. 1981. Hotade och sällsynta ryggradsdjur i Sverige 1980. SNV PM 1431, Statens naturvårdsverk, Solna, Sweden.
- Banci, V. 1987. Ecology and behaviour of wolverine in Yukon. M.Sc. thesis, Simon Fraser University, Vancouver, B.C.
- Banci, V. 1994. Wolverine. USDA For. Serv. Gen. Tech. Rep. RM254. pp. 99–127.
- Banci, V., and Harestad, A.S. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. Ann. Zool. Fenn. 25: 265–270.
- Björvall, A., and Isakson, E. 1982. Winter ecology of a pack of tree wolves in northern Sweden. In *Wolves of the world*. Edited by

- F.H. Harrington and P.C. Paquet. Noyes Publications, Park Ridge, N.J. pp. 146–157.
- Björvall, A., and Lindström, D. 1991. Vinterens däggdjur och fåglar i fjällvärlden, En 10-årig skoterinventering i Norrbotten ovan odlingsgränsen. Rep. No. 3919, Naturvårdsverket, Stockholm, Sweden.
- Björvall, A., Franzén, R., Nordkvist, M., and Åhman, G. 1990. Renar och rovdjur, rovdjurens effekter på rennäringen. Naturvårdsverket, Stockholm, Sweden.
- Box, G.E.P., Jenkins, G.M., and Reinsel, G.C. 1994. Time series analysis: forecasting and control. Prentice-Hall Inc., Englewood Cliffs, N.J.
- Børset, A. 1995. Forvaltning av freda rovvilt i Møre og Romsdal 1991–94. Fylkesmannen i Møre og Romsdal. Rep. No. 10, Molde, Norway.
- Grue, H., and Jensen, B. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. Dan. Rev. Game Biol. 11: 1–50.
- Haglund, B. 1966. De stora rovdjurens vintervanor. [Winter habits of the lynx (*Lynx lynx* L.) and wolverines (*Gulo gulo* L.) as revealed by tracking in the snow.] [In Swedish with English summary.] Viltrevy, 4: 81–310.
- Heggberget, T.M., and Myrberget, S. 1980. Bestanden av jerv i Norge i 1970-åra. [The wolverine *Gulo gulo* population in Norway in the 1970's.] [In Norwegian with English summary.] Fauna, 33: 52–55.
- Johnsen, S. 1928. Rovdyr og rovfuglstatistikken i Norge. Bergen Museums Årbok 1929, Naturvitenskapelig rekke 2, Bergen, Norway.
- Kruuk, H. 1972. Surplus killing by carnivores. J. Zool. (1965–1984), 166: 233–244.
- Kvam, T. 1979. Jervesporing i Snøhetta-Rondane våren 1979. Viltrapport 7, Norwegian Directorate for Nature Management, Trondheim.
- Kvam, T. 1980. Jervens status i Snøhetta-Rondane området i 1979 og 1980. [Population status of the wolverine *Gulo gulo* in some central Norwegian mountain areas.] [In Norwegian with English summary.] Fauna, 33: 117–127.
- Kvam, T., and Sørensen, O.J. 1981. Jervens status i Snøhetta, Rondane og en del omliggende fjellstrøk 1981. Viltrapport 19, Norwegian Directorate for Nature Management, Trondheim.
- Kvam, T., and Sørensen, O.J. 1983. Utviklingen i jervestammen i Snøhettaområdet i perioden 1979–1982. Arbeidsrapport 4, Norwegian Directorate for Nature Management, Trondheim.
- Kvam, T., Overskaug, K., and Sørensen, O.J. 1987. Jerveinventering i Snøhetta-området våren 1986. Rovviltrapport 1, Norwegian Directorate for Nature Management, Trondheim.
- Kvam, T., Overskaug, K., and Sørensen, O.J. 1988. The wolverine *Gulo gulo* in Norway. Lutra, 31: 7–20.
- Kålås, J.A., Framstad, E., Pedersen, H.C., and Strand, O. 1995. Terrestrisk naturovervåking, fjellrev, hare, smågnagere, fugl og næringskjedestudier i TOV-områdene, 1994. [Monitoring program for terrestrial ecosystems, Arctic foxes, mountain hares, small rodents, birds and food chain studies in the TOV areas, 1994.] [In Norwegian with English summary.] Oppdragsmelding 367, Norwegian Institute for Nature Research, Trondheim.
- Landa, A. 1986. Gaupe i Agder og Telemark. Arbeidsrapport 23, Norwegian Directorate for Nature Management, Trondheim.
- Landa, A., and Skogland, T. 1989. Bestandstelling av jerv i Snøhetta og omliggende fjell vinteren 1989. Oppdragsmelding 11, Norwegian Institute for Nature Research, Trondheim.
- Landa, A., and Skogland, T. 1995. The relationship between population density and body size of wolverines *Gulo gulo* in Scandinavia. Wildl. Biol. 1: 165–175.
- Landa, A., and Tømmerås, B.Å. 1996. Do volatile repellents reduce wolverine *Gulo gulo* predation on sheep?. Wildl. Biol. 2: 119–126.
- Landa, A., Krogstad, S., and Tømmerås, B.Å. 1996. Jervpredasjon på sau — Storskalaforsøk med lukt og smaksrepellenter 1996. [Wolverine predation on sheep—large scale experiment of volatile repellents 1996.] [In Norwegian with English summary.] Oppdragsmelding 451, Norwegian Institute for Nature Research, Trondheim.
- Loen, J. 1991. Store rovdyr i Sør-Trøndelag og jerven i Dovre/Rondane, 1991. Bestander, konflikter og tiltak. Rep. No. 7, Fylkesmannen i Sør-Trøndelag, Trondheim, Norway.
- Lönnerberg, E. 1936. Bidrag til järvens historia i Sverige. K. Sven. Vetenskapsakad. Skr. Naturskyddsarenden, 32: 1–38.
- Magoun, A.J. 1985. Population characteristics, ecology and management of wolverine in north-western Alaska. Ph.D. thesis, University of Alaska, Fairbanks.
- Magoun, A.J. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska, Can. Field-Nat. 101: 392–397.
- Mortensen, A.J. 1995. Forvaltning av fredet rovvilt i Oppland 1994. Rep. No. 7, Fylkesmannen i Oppland, Lillehammer, Norway.
- Myhre, R., and Myrberget, S. 1975. Diet of wolverines (*Gulo gulo*) in Norway. J. Mammal. 56: 752–757.
- Myrberget, S. 1968. Jervens ynglehi. The breeding den of the wolverine, *Gulo gulo*. [In Norwegian with English summary.] Fauna, 21: 108–115.
- Myrberget, S., and Grotnes, P. 1969. Sau og jerv i Jotunheimen. Nor. Nat. 5: 75–84.
- Myrberget, S., and Sørungård, R. 1975. Jervens og gaupas status i Norge. Naturen, 4: 170–174.
- Myrberget, S., and Sørungård, R. 1979. Fødselstidspunkt og kullstørrelse hos jerv. [Time of birth and litter size in wolverines.] [In Norwegian with English summary.] Fauna, 32: 9–13.
- Myrberget, S., Groven, B., and Myhre, R. 1969. Jervesporinger i Jotunheimen. [Tracking wolverines, *Gulo gulo*, in the Jotunheim Mountains, south Norway, 1965–68.] [In Norwegian with English summary.] Fauna, 22: 237–252.
- Oksanen, T., Oksanen, L., and Fretwell, S.D. 1985. Surplus killing in the hunting strategy of small predators. Am. Nat. 126: 328–346.
- Olstad, O. 1945. Jaktzoologi. Cappelen, Oslo. pp.128–226.
- Overskaug, K., Kvam, T., and Sørensen, O.J. 1986. Jerv i Norge 1985. Arbeidsrapport 28, Norwegian Directorate for Nature Management, Trondheim.
- Pulliainen, E. 1968. Breeding biology of the wolverines (*Gulo gulo*) in Finland. Ann. Zool. Fenn. 5: 338–344.
- Pulliainen, E. 1988. Ecology, status and management of the Finnish wolverine *Gulo gulo* populations. Lutra, 31: 21–28.
- Røskoft, E. 1988. Årsrapport Prosjekt jerv 1987. Økoforsk notat, 3, Trondheim, Norway.
- Semenov-Tjan-Shanskii, O. 1982. Zveri Murmanskoi Oblasti, Murmansk. [Mammals of Murmansk Oblast.] [In Russian; translated into Norwegian by the county governor of Finnmark, Norway.] Rep. No. 25, 1987, Vadsø, Norway.
- Skogland, T. 1985. The effects of density-dependent resource limitation on the demography of wild reindeer. J. Anim. Ecol. 54: 359–374.
- Skogland, T. 1988. Tooth wear by food limitation and its life history consequences in wild reindeer. Oikos, 51: 238–242.
- Skogland, T. 1989. Comparative social organisation of wild reindeer in relation to food, mates and predation avoidance. Adv. Ethol. No. 29.
- Skogland, T. 1994. Villrein, Fra urinnvåner til miljøbarometer. Teknologisk forlag, Oslo, Norway.
- Skogland, T., Strand, O., and Heim, M. 1991. Overvåking hjortevilt—rein. Årsrapport Hardangervidda og Snøhetta 1991. Oppdragsmelding 122, Norwegian Institute for Nature Research, Trondheim.
- Swenson, J.E., Wabakken, P., Sandegren, F., Björvall, A.,

- Franzén, R., and Söderberg, A. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildl. Biol.* 1: 11–25.
- Sørensen, O.J., and Kvam, T. 1986. Jerveundersøkelser i Snøhettaområdet i 1984. Arbeidsrapport 21, Norwegian Directorate for Nature Management, Trondheim.
- Sørensen, O.J., Kvam, T., Wabakken, P., and Landa, A. 1986. Ulven (*Canis lupus* L.) i Norge 1948–84. [The wolf (*Canis Lupus* L.) in Norway 1948–1984.] [In Norwegian with English summary.] Viltrapport 33, Norwegian Directorate for Nature Management, Trondheim.